

# Neotropical *Thrypticus* (Diptera: Dolichopodidae) Reared from Water Hyacinth, *Eichhornia crassipes*, and Other Pontederiaceae

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**ABSTRACT** Nine new species of *Thrypticus* (Diptera, Dolichopodidae) are described from South America: *T. truncatus*, *T. sagittatus*, *T. yanayacu*, *T. circularis*, *T. chanophallus*, *T. romus*, *T. azuricola*, *T. formosensis*, and *T. taragui*. All nine species were reared from the petioles and stems of aquatic and semiaquatic Pontederiaceae, five of them from water hyacinth, *Eichhornia crassipes*. These species appear to comprise the monophyletic *truncatus* Group characterized by a short and rather weakly sclerotised oviscapt, probably adapted to egg-laying in the soft petioles of Pontederiaceae. By contrast, most other *Thrypticus* species have a longer and more strongly sclerotised oviscapt for oviposition in hard-stemmed Poaceae, Cyperaceae, and Juncaceae. *T. truncatus* and *T. sagittatus* have potential as biological control agents for *Eichhornia crassipes*, which is a serious invasive weed in the Old World tropics. Notes are presented on the life history of these two species, based on field and rearing chamber observations.

**KEY WORDS** *Thrypticus*, Dolichopodidae, biological control, Pontederiaceae, *Eichhornia crassipes*

WATER HYACINTH, *Eichhornia crassipes* (Mart.) Solms-Laub., is native to the New World tropics. However, it was widely introduced as an ornamental, and has subsequently spread to become an invasive weed in the waterways of Africa, Asia and Australasia. This weed can cover freshwater lakes, block waterways and clog hydroelectric generators. Many Neotropical phytophagous insects are able to debilitate water hyacinth and limit its growth, but such natural control agents are largely absent in its adventive range.

To manage water hyacinth more effectively, the South American Biological Control Laboratory (SABCL), Buenos Aires, has been investigating potential control agents from its native habitat. Phytophagous insects have been reared from infested host plants collected in Argentina, Brazil and Peru. These rearings have focused primarily on *Eichhornia crassipes*, but other Pontederiaceae have also been studied: *Eichhornia azurea* (Swarz) Kunth, *Pontederia cordata* L., *Pontederia subovata* (Seub.) Lowden, and *Pontederia rotundifolia* L. Prominent among the phytophagous feeders on this family are species of the stem-mining dolichopodid fly genus *Thrypticus* Gerstaecker (Cordo et al. 2000).

These *Thrypticus* species were all reared from rather soft petioles and stems of Pontederiaceae. All other known larvae of *Thrypticus* have been reared from

hard-stemmed grass and sedge families, Poaceae, Cyperaceae and Juncaceae (Dyde 1993). Two points are worth noting here:

i). Some of the species are abundant and easily swept from aquatic Pontederiaceae across much of South America. However, only a few reared specimens of this group (the Trinidad *T. sagittatus* material) were found in large Neotropical *Thrypticus* holdings of several North American museums. This suggests that such emergent aquatic vegetation is rarely collected (deep water, slippery mud bottoms) and even large collections may totally lack common species from such "difficult" habitats.

ii). Initially, only one *Thrypticus* species was thought to be feeding on *Eichhornia crassipes*. However, with extensive collecting and rearing, SABCL researchers were able to discern five species (Cordo et al. 2000). Not only were these species separated by subtle yet distinct differences in genitalia, but also by differences in larval biology. However, if these species had been represented by only a few mounted specimens from desultory collecting (as are most described species), some of these interspecific differences might have been regarded as *intraspecific* variation. Many such species complexes can only be differentiated by long-term study, as in biological control rearings, where subtle differences are revealed by careful repeated observation.

In this paper, nine new species of South American *Thrypticus* are described. All were reared from the larval stage on Pontederiaceae, and associated ecological information is presented.

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## Materials and Methods

Almost all of the material presented here was collected and reared by researchers at (SABCL) - South American Biological Control Laboratory, Buenos Aires. Most of the material cited is stored in alcohol, and except where noted as dry or slide mounted specimens. Other specimen repositories use the following institutional abbreviations: (CNC) - Canadian National Collection of Insects, Agriculture and Agri-Food Canada, Ottawa; (USNM) - National Museum of Natural History, Smithsonian Institution, Museum, Washington, DC.

Morphological terminology follows McAlpine (1981) and Bickel (1986). Common features are listed in the introductory descriptions and not repeated unless needing clarification. Measurements are in millimetres. Wing length is the perpendicular distance to the apex from an imaginary extension of the humeral crossvein; wing width is the maximum measurement across the wing perpendicular to the long axis. The CuAx ratio is the length of the dm-cu crossvein/ distal section CuA. The position of features on elongate structures such as leg segments is given as a fraction of the total length, starting from the base. The ratios for the tarsomeres are given in the following formula: tarsomere 1/ 2/ 3/ 4/ 5. The following abbreviations and terms are used: I, II, III: pro-, meso-, metathoracic legs; C, coxa; T, tibia; F, femur; t, tarsus; t<sub>1-5</sub>, tarsomeres 1-5; ad, anterodorsal; av, anteroventral; dv, dorsoventral; pd, posterodorsal; pv, posteroventral.

## Taxonomy

### Genus *Thrypticus* Gerstcker

**Diagnosis.** Body length: 1.2-3.0 mm. Body coloration usually bright metallic green, sometimes with pale brown/ yellow abdominal segments, and usually with pale brown or pale yellow legs; eyes with short hairs between facets; thorax with two rows of short acrostichal (ac) setae; only one supraalar (sa) seta present; coxa III with two lateral setae; femur II with posterior subapical seta; humeral cross vein absent; veins R4 + 5 and M subparallel to apex; CuAx ratio usually <0.5; anal vein absent; hypandrium arising basoventrally from epandrium, and sometimes with flexion or indentation in distal third; aedeagus (=phallus) usually bifurcate apically; epandrium curved, basal, and arising within epandrial chamber, not visible in lateral view; epandrial lobes fused into elongate collar from which two apical setae arise; surstylus sometimes deflexed dorsally, and lying conformably with similarly deflexed oblong cercus; cercus elongate; female oviscapt blade-like, sclerotized, narrow in dorsal view, with serrated apical aculeus.

**Remarks.** The genus *Thrypticus* is a member of the dolichopodid subfamily Medeterinae and has a sister group relationship with the genus *Corindia* Bickel (Bickel 1986). The Medeterinae are separated from other dolichopodid subfamilies by the following combination of characters: posterior mesoscutum dis-

tinctly flattened; femora II and III lacking anterior preapical setae; tibiae mostly bare of strong setae; hypopygium large and exerted, on peduncle formed by abdominal segment seven (Fig. 1); antennal scape without dorsal setae; and, dorsal postcranium strongly concave.

*Thrypticus* is distinguished within the subfamily by: female oviscapt blade-like, sclerotized, narrow in dorsal view; CuAx ratio usually <0.5, i.e., crossvein dm-cu somewhat distant from posterior margin of wing.

*Thrypticus* is unique in the family Dolichopodidae, and indeed among the lower Diptera Brachycera, the "Orthorrhapha," in having phytophagous stem-mining larvae. Correspondingly, the female oviscapt of *Thrypticus* has been modified into a sclerotised blade for piercing and ovipositing within plant tissue. This synapomorphy not only defines the genus, but also constitutes a key innovation in a shift away from ancestral predation/ saprophagy to larval feeding within living plant tissue. Parallel development of a sclerotised plant piercing oviscapt is evident in other dipteran families, notably the fruit fly family Tephritidae.

The relatively small-sized *Thrypticus* adults are frequently collected sweeping marshland and emergent aquatic vegetation. All known *Thrypticus* larvae are miners in aquatic and semiaquatic monocotyledons, and species have been reared from the following genera (Dyde 1993, and records here): Cyperaceae: *Eleocharis* and *Scirpus*; Juncaceae: *Juncus*; Poaceae: *Mulhenbergia*, *Phragmites*, and *Spartina*; Pontederiaceae: *Eichhornia* and *Pontederia*. Larval nutrition is probably a combination of plant sap and the bacteria and yeasts growing in the plant wound.

*Thrypticus* is cosmopolitan, with some 86 described species: 48 from the New World (including the nine species described here), eight Afrotropical, 24 Palearctic, two Oriental, and four from Australia and New Zealand. The genus displays greatest diversity and morphological disparity in the Neotropical Region, where numerous species await description.

The species of *Thrypticus* found growing on *Eichhornia* and *Pontederia* comprise the *truncatus* group. This group is probably monophyletic, supported by the structure of the oviscapt and male abdomen, and is named for *T. truncatus*, the most abundant species on *E. crassipes*.

### The *truncatus* Group

**Diagnosis.** Body length: 1.2-1.4 mm. Body coloration usually metallic green or brown with metallic green reflections, sometimes with yellow or brownish abdominal segments; legs pale brown or pale yellow; antenna mostly yellow; tibia II without ad setae; hypandrium, without flexion in distal half; surstylus not strongly deflexed dorsally, male cercus distally elongate, and free, not appressed to or conforming to shape of surstylus; oviscapt (Fig. 5a and b) narrow and rather weakly sclerotised; aculeus rather short, and not strongly melanized; oviscapt and abdominal segments not able to be extended more than shown in Fig. 5.

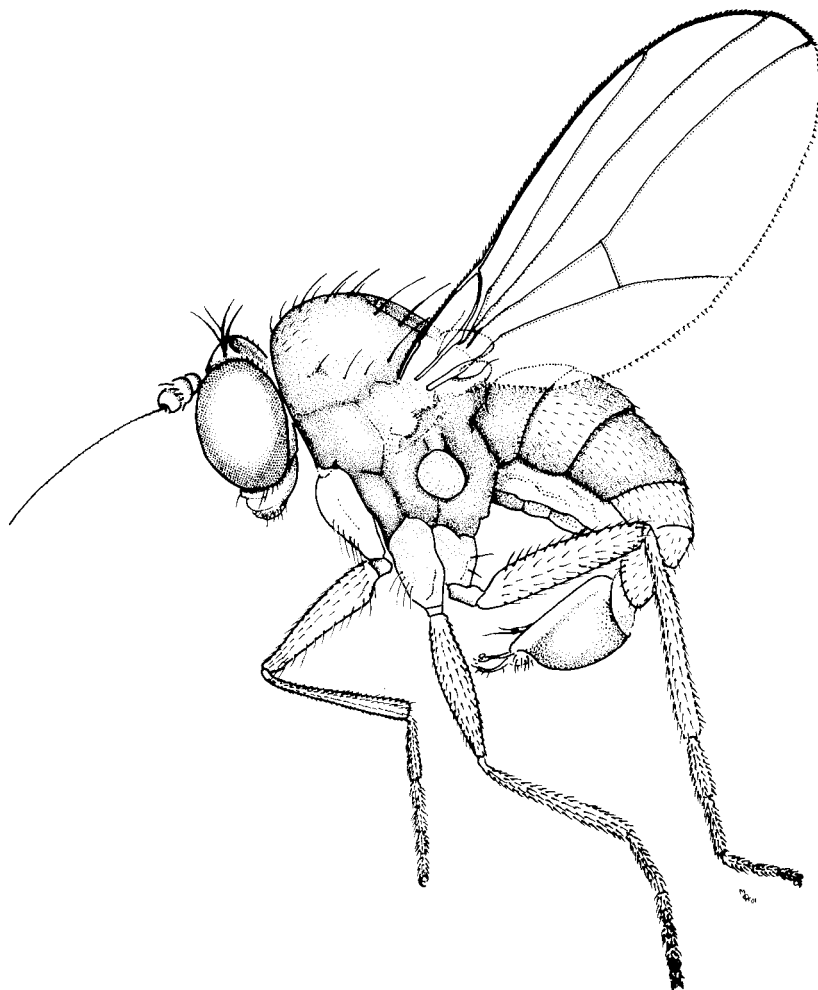


Fig. 1. *Thrypticus truncatus* sp. n. male, habitus.

**Remarks.** The *Thrypticus truncatus* Group comprises nine Neotropical species, all newly described: *T. truncatus*, *T. sagittatus*, *T. yanayacu*, *T. romus*, *T. azuricola*, *T. formosensis*, *T. taragui*, *T. circularis*, and *T. chanophallus*. All species were reared from the petioles and stems of aquatic and semiaquatic Pontederiaceae, five of them from water hyacinth, *Eichhornia crassipes*.

The *truncatus* Group is characterized by a short and rather weakly sclerotised oviscapt, probably adapted for oviposition in the relatively soft parenchyma of Pontederiaceae. By comparison, many other *Thrypticus* (e.g., the group of species near the Palearctic *T. bellus* Loew, and the widespread New World *T. fraterculus* Wheeler) have strong heavily sclerotised oviscapt with a hard aculeus designed to pierce the tough stems of grass-like monocotyledons.

The aculeus or apex of the *Thrypticus* oviscapt often has a shape and serration that can be diagnostic for species level identification. The aculeus is figured for seven of the nine *truncatus* Group species (Figs. 2e, 2j,

3e, 3j, 3o, 4e, 4k). Although diagnostic identification based on the serration pattern of the aculeus is possible, further investigation is required, as differences are subtle.

**Phylogenetic position.** Although this is not the place to discuss the evolution of *Thrypticus*, at least two characters of the *truncatus* Group should be discussed.

1. The male cercus is elongate distally, and free, neither appressed to nor conforming to the shape of the surstylus. This condition could be regarded as plesiomorphic, as most other Medeterinae have "free" cerci, and the appressed cercus of the *bellus* Group and other *Thrypticus* species should be seen as a derived state.

2. The oviscapt is rather weakly sclerotised and melanized, and unlike most other *Thrypticus* species, the retracted preabdominal segments are difficult to extract without tearing the segments. (The maximum abdominal exsertion in alcoholic specimens is illustrated in Figs. 5a and b; by contrast, one can easily pull out the retracted abdominal segments in such species

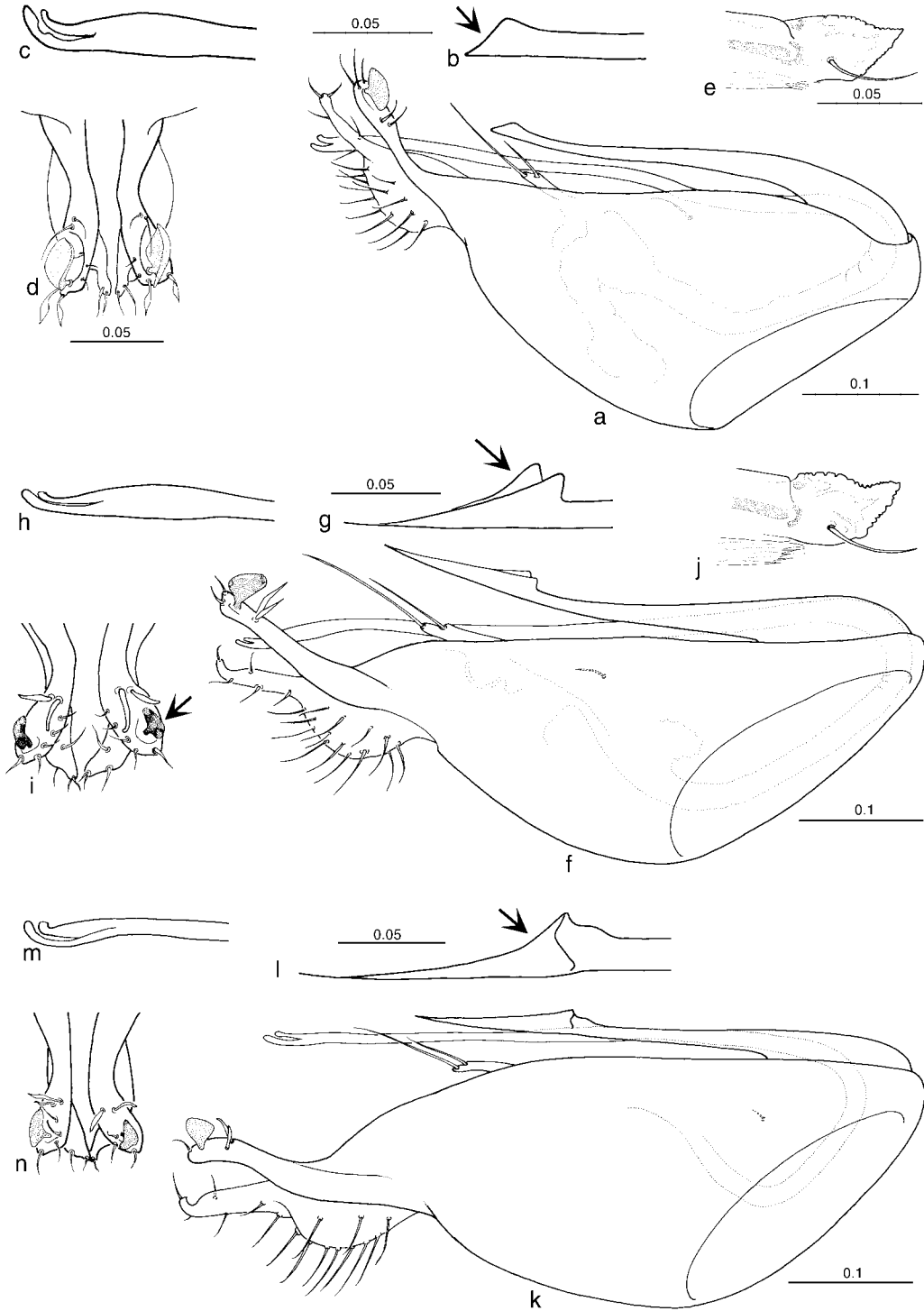
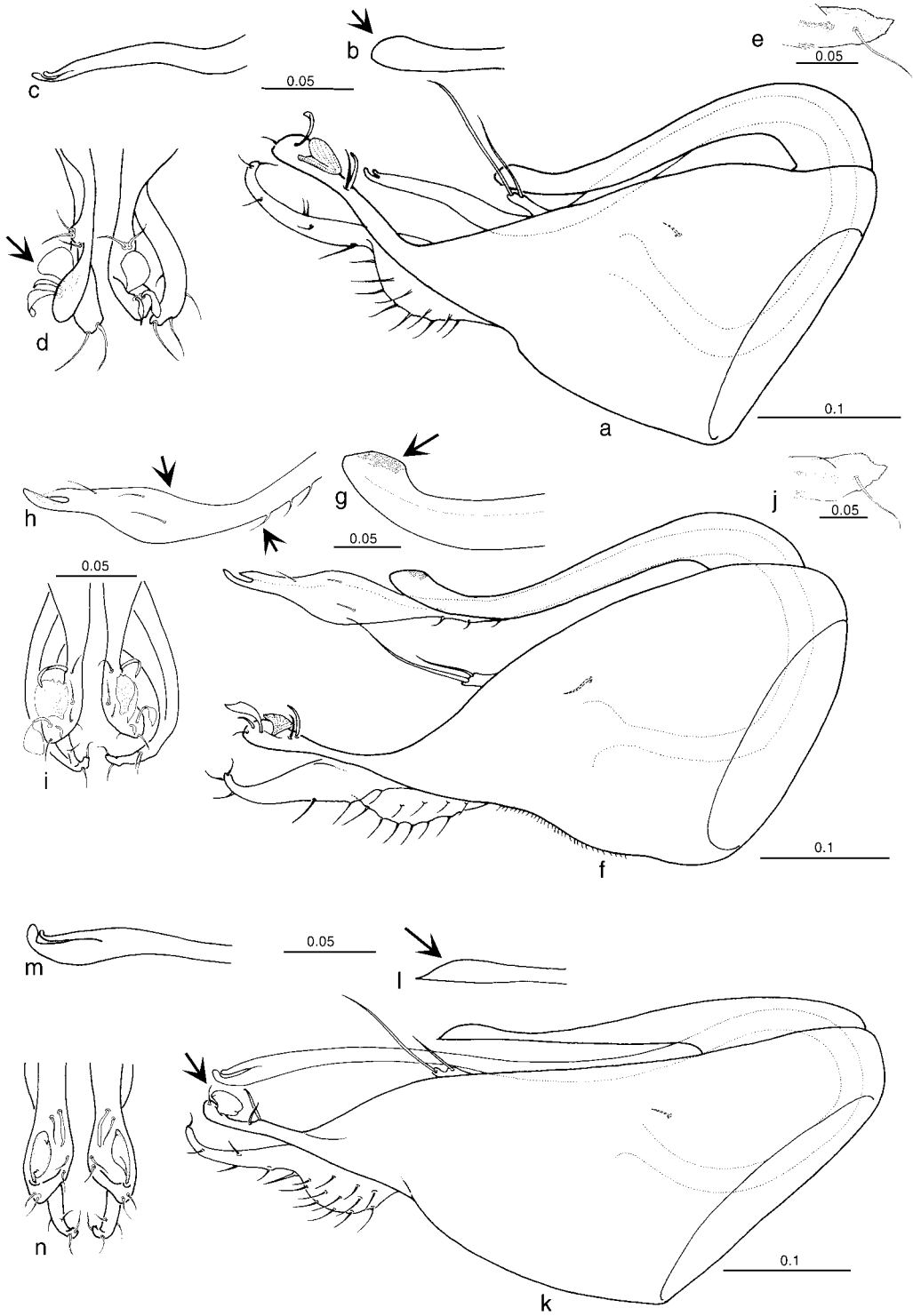


Fig. 2. *Thrypticus truncatus*: a. hypopygium, left lateral; b. hypandrium., left lateral; c. aedeagus left lateral; d. distal surstyli and cerci, ventral; e. aculeus of oviscapt, left lateral. *T. sagittatus*: f. hypopygium, left lateral; g. hypandrium., left lateral; h. aedeagus, left lateral; i. distal surstyli and cerci, ventral; j. aculeus of oviscapt, left lateral. *T. yanayacu*: k. hypopygium, left lateral; l. hypandrium., left lateral; m. aedeagus left lateral; n. distal surstyli and cerci, ventral. [Arrows indicate important diagnostic features].



**Fig. 3.** *Thrypticus romus*: a. hypopygium, left lateral; b. hypandrium., left lateral; c. aedeagus left lateral; d. distal surstyli and cerci, ventral; e. aculeus of oviscapt, left lateral. *T. azuricola*: f. hypopygium, left lateral; g. hypandrium., left lateral; h. aedeagus, left lateral; i. distal surstyli and cerci, ventral; j. aculeus of oviscapt, left lateral. *T. formosensis*: k. hypopygium, left lateral; l. hypandrium., left lateral; m. aedeagus left lateral; n. distal surstyli and cerci, ventral; o. aculeus of oviscapt. [Arrows indicate important diagnostic features].

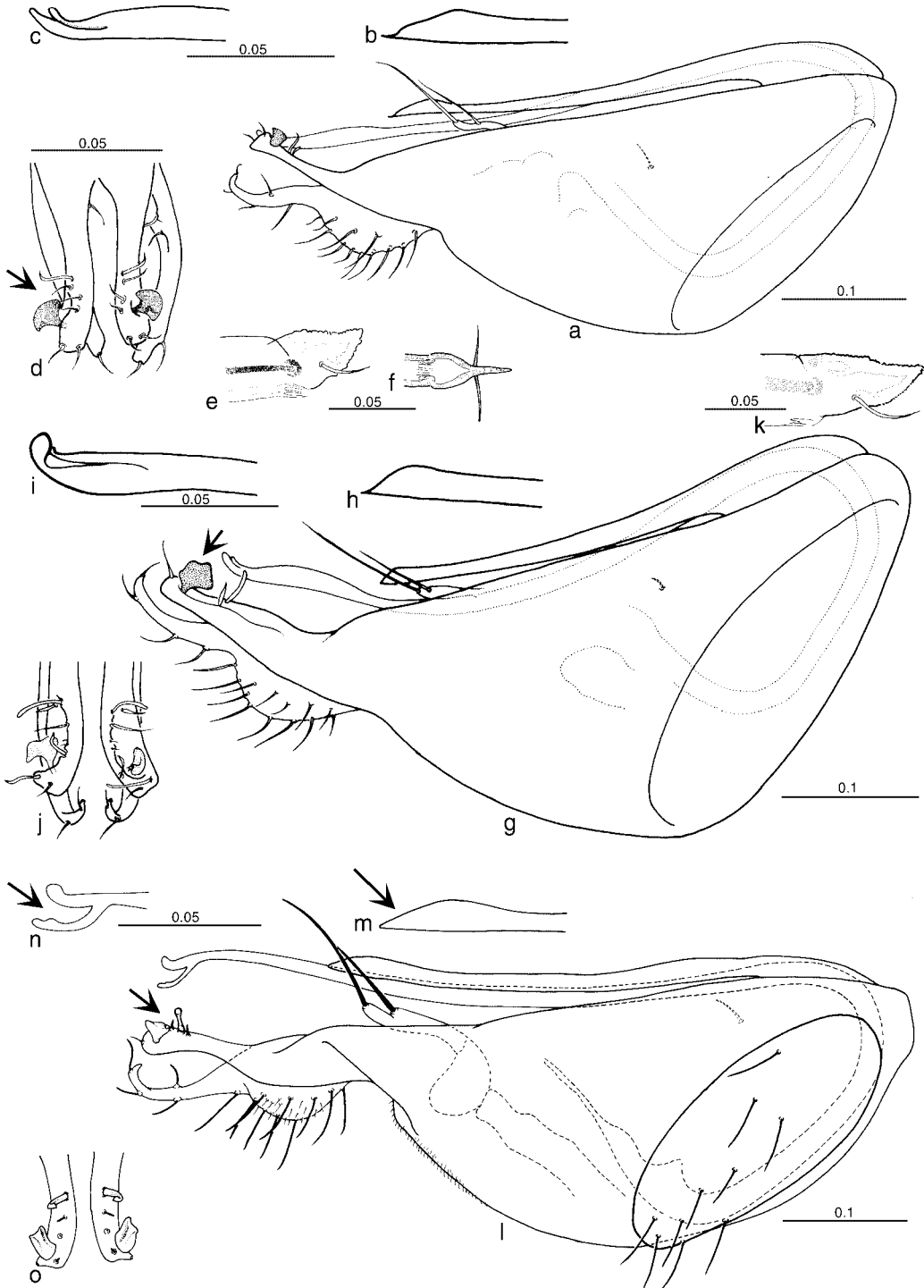


Fig. 4. *Thrypticus circularis*: a. hypopygium, left lateral; b. hypandrium., left lateral; c. aedeagus, left lateral; d. distal surstyli and cerci, ventral; e. aculeus of oviscapt, left lateral; f. aculeus of oviscapt, dorsal. *T. taragui*: g. hypopygium, left lateral; h. hypandrium., left lateral; i. aedeagus left lateral; j. distal surstyli and cerci, ventral; k. aculeus of oviscapt, left lateral. *T. chanophallus*: l. hypopygium with sternite eight attached, left lateral; m. hypandrium., left lateral; n. aedeagus, left lateral; o. distal surstyli, ventral. [Arrows indicate important diagnostic features].



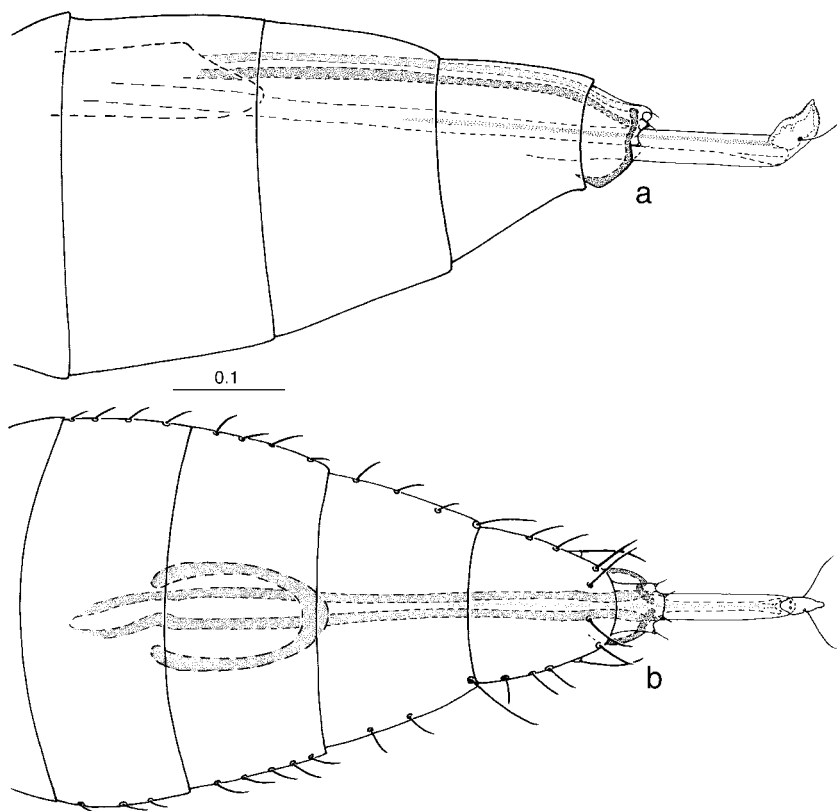


Fig. 5. *Thrypticus truncatus* sp. n., female abdomen. a. left lateral; b. dorsal.

as *T. fraterculus*). The relatively short weakly sclerotised oviscapt is possibly adapted for oviposition in the soft petioles of Pontederiaceae. However, it could also be regarded as an intermediate state in the further development of a plant piercing oviscapt, or the *bauplan* upon which more heavily sclerotised oviscapts could develop to penetrate tougher plant tissues.

Therefore, in regard to the two points above, the *truncatus* Group could be regarded alternatively as the rather plesiomorphic sister group or the paraphyletic stem group to the rest of *Thrypticus*. Its presence in the Neotropics may not be accidental, not only reflecting the current species richness of *Thrypticus* in that region, but the genus itself could have arisen in the vast areas of emergent aquatic vegetation along the Orinoco, Amazon, and Paraná floodplains.

#### Key to *Thrypticus truncatus* Group species

For accurate species identification, male genitalia usually need to be cleared and slide mounted for examination with a compound microscope.

1. Oviscapt (Fig. 5a and b) rather weakly sclerotised; aculeus rather short, and not strongly melanized; oviscapt and abdominal segments not able to extend more than shown in Fig. 5; male cercus distally elongate, and free, not appressed to or conforming with shape of

surstylus; tibia II without ad seta; surstylus elongate; hypandrium without flexion (ex. Pontederiaceae). *truncatus* Group . . . . . 2

-Oviscapt usually strongly sclerotised; aculeus often elongate and melanized; oviscapt and preabdominal segments often able to extend greatly; male cercus often lobate and appressed and conforming to shape of surstylus; tibia II usually with ad seta; surstylus lobate; hypandrium often with distinct flexion from one-half to three-fourths (ex. Poaceae, Cyperaceae, or Juncaceae, where known). . . . . other *Thrypticus*

2. Hypandrium apically blunt, not pointed (Fig. 3b and g); epandrium wide at base and tapering distally (Figs. 3a and f); terga 1–4 metallic green with bronze reflections (ex. *Eichhornia azurea*). . . . . 3
- Hypandrium tapering to point (e.g., Figs. 2a and f); epandrium usually more elongate; tergal coloration various . . . . . 4
3. Aedeagus (Fig. 3h) broadened subapically, and with setae as shown; cercus thickened and curved apically (Fig. 3f); hypandrium (Fig. 3g) somewhat thickened and melanized apically . . . . . *T. azuricola*
- Aedeagus (Fig. 3c) not broadened, but with gentle U-shaped bend, and bare of setae; cer-

- cus elongate and curved apically (Fig. 3a); hypandrium (Fig. 3b) blunt and not melanized apically . . . . . *T. romus*
4. Hypandrium with long tapering apex and distinct prominence about one quarter distance from apex (Figs. 2f and k); tergum one only metallic green with bronze reflections; terga 2–6 brownish with metallic green reflections. . . . . 5
- Hypandrium with more abrupt apex (e.g., Figs. 3l, 4m), and with even surface, without distinct prominence; abdominal tergal coloration various . . . . . 6
5. Hypandrium (Fig. 2g) with lateral "wings" about one quarter distance from apex; distal surstylus (Fig. 2i) with black striated fan-shaped seta (ex. *Eichhornia crassipes*) . . . *T. sagittatus*
- Hypandrium (Fig. 2l) with distinct thickened crest about one third distance from apex, without lateral "wings"; distal surstylus (Fig. 2n) with pale fan-shaped seta (ex. *E. crassipes*) . . . . . *T. yanayacu*
6. Aedeagus (Fig. 4n) with distinctive open apex, encompassing 45 deg. angle; distal surstylus (Fig. 4o) with subapical bladeli-like seta, subtended basad by peg-like apically curved seta; hypopygium as in Fig. 4l (ex. *E. crassipes*) . . . . . *T. chanophallus*
- Aedeagus (e.g., Figs. 2c, 3m, 4c, 4i) with apical arms more or less subparallel; distal surstylus with subapical bladeli-like or fanlike seta not subtended by peg-like seta . . . . . 7
7. Hypandrium (Fig. 2b) slightly enlarged subapically and truncated to apex with 45 degree slope; hypopygium as in Fig. 2a; surstylus (Fig. 2d) with pale blade-like seta with thickened setae distad; terga 1–3 metallic green with bronze reflections (ex. *E. crassipes*) . . . . . *T. truncatus*
- Hypandrium not so distinctly apically truncated; other characters various . . . . . 8
8. Hypandrium (Fig. 3k) relatively short, not extending beyond epandrial lobes; aedeagus (Fig. 3m) apically cleft, with lower arm thickened and bent L-shaped across tip of upper arm; hypopygium as in Fig. 3k (ex. *Pontederia cordata*) . . . . . *T. formosensis*
- Hypandrium extending well beyond base of epandrial lobes; apex of aedeagus various . . . 9
9. Hypandrium (Fig. 4h) with slightly truncated apex; aedeagus (Fig. 4i) apical cleft with thick lower apical arm bent in L-shape in front of narrower upper arm; hypopygium as in Fig. 4g (ex. *Pontederia subovata*) . . . . . *T. taragui*
- Hypandrium (Fig. 4b) more gradually tapered to apical point; aedeagus (Fig. 4c) apical cleft with both arms subparallel and slightly curved upward; hypopygium as in Fig. 4a (ex. *E. crassipes*) . . . . . *T. circularis*

**Descriptions.** All of the material described below was directly reared from host plants, and most is in alcohol. Although newly emerged specimens were

allowed to develop for at least 24 h before preservation (Cordo et al. 2000), many appear rather pale colored and somewhat faded. Since specimens captured from nature will often appear darker, live color if known, is also noted. However, the diagnostic species characters are based on the male genital structure. In any case, overall coloration and body characters are similar among *truncatus* Group species.

#### *Thrypticus truncatus* sp. n.

**Type material.** Holotype, ♂, Paratype ♀ (collected as mating pair): ARGENTINA: Formosa, Palo Santo, 6.i.2001, emerged from *Eichhornia crassipes*, H. Cordo. (SABCL, deposited USNM). Paratypes: same as holotype except as noted: 12 ♂, 6 ♀, 20.xii.1999; 4 ♂, 6 ♀, 23.ii.1998; 4 ♂, 9 ♀, 6.i.2001 (SABCL).

**Additional material.** ARGENTINA: Buenos Aires: 3 ♂, 2 ♀, Otamendi, 24.iii.1997 (CNC); 5 ♂, Tigre, 20.iii.1997; Chaco: 4 ♂, 2 ♀, Rd.5, 4km SW to Villa Río Bermejo, 26.ii.1998 (SABCL); 2 ♂, ♀, Rd.16, 25 km Macalle, Estero Chajá, 26.iii.1997 (SABCL); 3 ♂, Resistencia, Rt 16, 12.xii.1997 (USNM); ♂, Río Tragadero, road to Isla del Cerrito, 12.xii.1997 (USNM); ♂, 39 miles W Resistencia, Rt 16, 12.xii.1997 (USNM); 2 ♂, 4 ♀, Rt 11, 8 miles N Basail, 15.xii.1997 (USNM). Corrientes: 3 ♂, 4 ♀, Paso de la Patria, pond on road to Rt. 12, 16.iv.1996 (USNM). Formosa: 3 ♂, ♀, Pirané, 27.x. 2000 (SABCL). BRAZIL: São Paulo: 2 ♂, 3 ♀, SP55, Yuquehy, 13.iv.2000. Río Grande do Sul: 5 ♂, 3 ♀, BR101, 5km S Capao da Canoa, 9.iv.2000; Paraná: ♂, Foz do Iguassu, 23.iv.2000. PERU: Loreto: 2 ♂, Río Marañon, 04°30'38" S 73°32'42" W, 1.v.1999; ♂, Montoya, Cocha, 04°31'00"S 73°32'23"W, 3.v.1999; ♂, Río Nanay, 5.v.1999, 03°41'48"S 73°14'34"W (SABCL) (all specimens emerged from *Eichhornia crassipes* and collected by H. Cordo).

**Description.** Male. Body length 1.4–1.5; wing 1.4 by 0.5 (Fig. 1, habitus)

**Head.** vertex, occiput, frons and face metallic blue green with dusting of gray pruinosity; major setae yellowish; pairs of strong vertical, postvertical and ocellar setae present; eyes in life iridescent green with red reflections, and distinctly separated along face; palp brown; proboscis pale brown; scape and pedicel yellow; postpedicel mostly brown, but base yellowish; arista apical, slightly longer than head height.

**Thorax.** metallic green with bronze reflections, and with dusting of silvery-gray pruinosity; scutellum dorsally metallic green but becoming yellow around margin, and ventrally yellow; setae yellowish; field of setulae present anteriad of mesonotal suture and laterad of dc row; eight pairs of short acrostichal (ac) setae present, increasing in size posteriorly, with posterior-most pair laterally offset; five dorsocentral (dc) setae present; one postalar, only one postsutural supra-alar, one postpronotal, one presutural supra-alar, one presutural intra-alar, and two notopleural setae present; median scutellar setae strong, laterals reduced short side hairs; propleural setae absent.

**Legs.** coxa I yellow; coxae II and III brown, becoming pale brown apically; all trochanters and remainder



of legs light brown; vestiture yellow; coxae I and II with short anterior setae; coxa III with two pale lateral setae, dorsal longer than ventral; leg I: 8.9/ 4.1/ 3.6/ 2.8/ 3.6; II: 12.5/ 6.9/ 5.5/ 3.3/ 3.5; FII with posterior subapical seta; TII bare of anterodorsal setae; TII with short apicoventral seta; III: 9.2/ 10.2/ 6.5/ 3.8/ 3.8.

**Wing.** R4 + 5 and M beyond dm-cu crossvein subparallel to apex, and both slight arched anteriorly; CuAx ratio: 0.45; lower calypter pale yellow with pale yellow setae; halter pale yellow.

**Abdomen.** terga 1–3 metallic green with bronze reflections and some gray pruinosity; terga 4–5 dark brown with metallic green reflections; terga six and seven brownish; vestiture yellow; sternum eight dark brown with metallic green reflections; hypopygium (Fig. 2a) dark brown with yellow cerci; epandrium pyriform, narrowed distally; hypandrium (Fig. 2b) slightly enlarged subapically and truncated to apex with 45 degree slope; aedeagus (Fig. 2c) with apex cleft and both arms curved; epandrial seta arising from lateral walls of genital chamber, not visible externally; epandrial lobes fused into collar, bearing two distal setae; surstylus (Fig. 2d) with pale fan-shaped seta with thickened setae distad; cercus elongate and curved apically.

**Female.** similar to male except face slightly wider; abdomen (Figs. 5a and b) with segment seven (forming the oviscapt sheath) brown; oviscapt brownish, narrow; aculeus (Fig. 2e).

**Remarks.** *Thrypticus truncatus* is known from the Río Paraná drainage, southeastern Brazil and Argentina as far south as Buenos Aires Province, and from Amazonian Peru, in the region around Iquitos. All specimens were reared from the petioles of *Eichhornia crassipes*, and this species is probably widespread in association with its host.

The truncate apex of the hypandrium is diagnostic, and is the source of the specific epithet. In both sexes, terga 1–3 are metallic green with bronze reflections, in contrast to the sympatrically occurring *T. sagittatus*, where only tergum one is metallic green-bronze. This abdominal color can be used to visually separate the two species in the field.

Both *Thrypticus truncatus* and *T. sagittatus* are widely sympatric, and have been reared together from *Eichhornia crassipes* taken in the same collecting event at many sites in Argentina and Brazil. However, it is not clear if both species have been reared from the same individual petioles. Possibly there exists distinct resource, behavioral or temporal niche separation between the two species on the same plant.

### *Thrypticus sagittatus* sp. n

**Type material.** Holotype ♂, Paratypes 3 ♂, 4 ♀: ARGENTINA: Formosa: Rt 81, 42 km W Formosa City, 14.iv.1996, emerged from *Eichhornia crassipes*, H. Cordo, Acc 413833 [dry mounted] (USNM)

**Additional material.** ARGENTINA: Buenos Aires: 6 ♂, 2 ♀, Tigre, 20.iii.1997 (3 ♂ to CNC); 2 ♂, Otamendi, 24.iii.1997. Chaco: 3 ♂, 4 ♀, Resistencia, Rt 16, 200m east jct. Rt 11 and Rt. 16, 12.xii.1997, ex. *Eichhornia*

*crassipes* (USNM) [dry mounted]; 4 ♂, 3 ♀, Rd.5, 4 km SW to Villa Río Bermejo. 26.ii.1998; ♂, Rd.16, 25 km Macalle, Estero Chajá. 26.ii.1997; ♂, 3 ♀, Barranqueras. 22.ii.1996. Formosa: 12 ♂, 5 ♀, Palo Santo, 20.xii.1999; 23 ♂, 34 ♀, Palo Santo, 6.i.2001; 4 ♂, 5 ♀, (dark colored), Palo Santo, iii.2001; 4 ♂, 5 ♀, (pale colored), Palo Santo, iii.2001. BRAZIL: Paraná: 5 ♂, Foz do Iguassu, 23.iv.2000. Río de Janeiro: ♂, Cabo Frio, 16.iv.2000. Río Grande do Sul: 4 ♂, 2 ♀, BR101, 5 km S Capao da Canoa, 9.iv.2000. São Paulo: 3 ♂, 3 ♀, SP55, Yuquehy, 13.iv.2000; 6 ♂, 3 ♀, Humaitá, 13.iv.2000. (all preceding specimens emerged from *Eichhornia crassipes*, H. Cordo, SABCL). TRINIDAD (dry mounted): 3 ♂, ♀, Penal, iii. 1972, in *Eichhornia*; ♂, ♀, Curepe, iv.1972, in *Eichhornia* stems (petioles?) (SABCL); 2 ♂, 2 ♀, Curepe, vi.1974, ex. *Eichhornia crassipes*, F.D. Bennett (USNM).

**Description.** Male. Body length 1.4; wing 1.3 by 0.5; similar to *T. truncatus* except as noted:

**Head.** eyes in life iridescent with green reflections.

**Legs.** leg I: 8.5/ 4.7/ 4.0/ 3.3/ 4.0; leg II: 13.1/ 8.0/ 5.3/ 3.5/ 3.5; leg III: 8.0/ 10.2/ 6.0/ 3.8/ 3.6.

**Wing.** CuAx ratio: 0.5

**Abdomen.** tergum one only metallic green with bronze reflections; terga 2–5 brown with metallic green reflections; terga six and seven yellowish; sternum eight brown with metallic green reflections; hypopygium (Fig. 2f) brown with yellow cerci; epandrium pyriform, narrowed distally; hypandrium (Fig. 2g) tapering apically to point, and with two lateral “wings” about one quarter from apex; aedeagus (Fig. 2h) with apex cleft and both arms subparallel and projecting distally; surstylus (Fig. 2i) with dark fan-shaped striated seta, with two thickened setae basad; cercus elongate and curved apically.

**Female.** similar to male except face slightly wider; abdomen mostly yellow; oviscapt brownish, narrow; aculeus (Fig. 2j).

**Remarks.** *Thrypticus sagittatus* is known from the Río Paraná drainage, southeastern Brazil and Argentina south to Buenos Aires Province, and also from Trinidad, near the coast of Venezuela. This suggests the species is widespread in eastern South America, always in association with *Eichhornia crassipes*. It is sympatric with *T. truncatus* at many sites in Argentina and southeastern Brazil.

Here it should be noted that the Trinidad specimens were incorrectly identified as *Thrypticus insularis* Van Duzee (= *T. minutus* Parent), and are variously cited under these names in Bennett (1976), Dyte (1993) and Cordo et al. (2000).

The hypandrium with its sharp apex and lateral “wings” is diagnostic, and its arrow-like appearance is the source of the specific epithet (*sagitta* is Latin for arrow). Another useful character is the black, striated fan-shaped seta positioned distally on the pale yellow surstylus, and is visible even on dried specimens. And in contrast to *T. truncatus*, this species has only tergum one (in both sexes) with metallic silvery-green coloration.

In some rearings (e.g., the Palo Santo series), specimens of both sexes appear to be darker than normal.

However, the hypopygium and oviscapt are identical among this material.

### *Thrypticus yanayacu* sp. n

**Type material.** Holotype ♂, PERU: Loreto: Río Nanay, 03°38'50" S 73°30'02" W, 5.v.1999; emerged from *Eichhornia crassipes*, H. Cordo. (USNM).

**Additional material.** PERU: Loreto: 3 ♂, Río Nanay, 03°41'48"S 73°14'34"W, 5.v.1999; 3 ♂, 2 ♀, Río Yanayacu, 04°16'41"S 73°16'09"W, 29.iv.1999; ♂, Río Marañón, 04°26'38" S 73°29'34" W, 1.v.1999; 2 ♂, Montoya, Cocha, 04°31'00" S 73°32'23" W, 3.v.1999; 3 ♀, not assigned, Montoya Cocha, 04°31'00" S 73°32'23" W; 3.v.1999 (all emerged from *Eichhornia crassipes*, H. Cordo (SABCL)).

**Description.** Similar to *T. truncatus* except as noted. Male. Body length 1.3–1.4; wing 1.2–1.3 by 0.5.

**Head.** antenna yellow.

**Thorax.** scutellum with only faint yellow margin.

**Abdomen.** tergum one only metallic green with bronze reflections; terga 2–6 brownish with metallic green reflections; terga 6–8 brown with metallic green reflections; hypopygium (Fig. 2k) brown with yellow cerci; epandrium elongate pyriform, narrowed distally; hypandrium (Fig. 2l) apically pointed, and gradually tapering, with distinct thickened crest about one third distance from apex; aedeagus (Fig. 2m) apically cleft with two narrow parallel arms, lower arm longer; surstylus (Fig. 2n) with fan-shaped seta; cercus rather wide distally, curved apically.

**Female.** not clearly associated.

**Remarks.** *Thrypticus yanayacu* is known from the upper Amazon drainage near Iquitos district of Peru, and all specimens were reared from the petioles of *Eichhornia crassipes*. It occurs sympatrically with *T. truncatus*, *T. chanophallus*, and *T. circularis* so that females cannot be accurately associated. The specific epithet is from an indigenous place name, Río Yanayacu, where some of the specimens were collected.

### *Thrypticus circularis* sp. n

**Type material.** Holotype, ♂, paratypes 6 ♂, PERU: Loreto: Río Marañón, 04°30'38" S 73°32'42" W, 3.v.1999, emerged from *Eichhornia crassipes*, H. Cordo (USNM).

**Additional material.** ARGENTINA: Formosa: ♂, Palo Santo, 27.xi.1999, emerged ex. inflated petiole of *E. crassipes*. PERU: Loreto: ♂, (3 ♀ not assigned) Río Yanayacu, 04°16'41"S 73°16'09"W, 29.iv.1999; 2 ♂, Río Marañón, 04°26'38" S 73°29'34" W, 1.v.1999; 4 ♂, (9 ♀, not assigned) Montoya Cocha, 04°31'00" S 73°32'23" W, 3.v.1999; 3 ♂, Río Nanay, 03°38'50" S 73°30'02" W, 5.v.1999; 5 ♂, (4 ♀ not assigned), Río Nanay, 03°40'55"S 73°40'44"W, 3.v.1999; 3 ♂, Río Nanay, 03°41'48"S 73°14'34"W, 5.v.1999; ♂, Río Marañón, 04°26'38" S 73°29'34" W, 1.v.1999 (all reared ex *Eichhornia crassipes*, H. Cordo, SABCL).

**Description.** Similar to *T. truncatus* except as noted. Male. Body length 1.3–1.4; wing 1.3 by 0.5.

**Head.** postpedicel apically brownish.

**Thorax.** scutellum without yellow margin.

**Abdomen.** terga 1–3 metallic green with bronze reflections and some gray pruinosity; terga 4–5 brown with metallic green reflections; terga six and seven brownish or even yellowish; hypopygium (Fig. 4a) brown with yellow cerci; epandrium pyriform, narrowed distally; hypandrium (Fig. 4b) slightly enlarged subapically but gradually tapering to apical point; aedeagus (Fig. 4c) with apex cleft and both arms subparallel and slightly curved; surstylus (Fig. 4d) with widened almost semicircular seta with some thickened setae basad; cercus elongate and becoming curved and narrower apically.

**Female.** similar to male except face slightly wider; segment seven (forming the oviscapt sheath) brown; oviscapt brownish, narrow; aculeus (Figs. 4e and f).

**Remarks.** *Thrypticus circularis* is known from the Iquitos District in Amazonian Peru, and the Río Paraná catchment in Argentina (also see discussion below). All specimens were reared only from the globose inflated petioles of *Eichhornia crassipes*, which function as a bulbous float to facilitate vegetative dispersal and colonization under certain environmental conditions. The specific epithet refers to the distinctive circular shape of the larval burrow in these inflated petioles. Females were described based on individuals reared from the circular mines.

In the southern reaches of the Río Paraná, inflated petioles with characteristic *Thrypticus circularis* mines have been collected and incubated, but no adults emerged [collections: Argentina: Entre Ríos: Villa Urquiza, 23.iv.2001; Buenos Aires: Río Sagastume, Delta Río Paraná, 5.iv.2002, all SABCL]. The Buenos Aires region is temperate and near the southern limit of *Eichhornia crassipes*. Possibly *T. circularis* larvae arrive periodically in floating petioles from the north, but are unable to survive the cooler conditions and establish local breeding populations.

### *Thrypticus chanophallus* sp. n

**Type material.** Holotype ♂, Paratypes 2 ♂, PERU: Loreto: Río Marañón, 04°26'38" S 73°29'34" W, 1.v.1999, emerged from *Eichhornia crassipes*; H. Cordo (USNM).

**Additional material.** PERU: Loreto: 3 ♂, Río Nanay, 03°41'48"S 73°14'34"W, 5.v.1999; 2 ♂, (2 ♀, not assigned), Río Marañón, 04°30'38" S 73°32'42" W, 3.v.1999 (all emerged from *E. crassipes*, H. Cordo, SABCL).

**Description.** Similar to *T. truncatus* except as noted. Male. Body length 1.3–1.4; wing 1.1–1.3 by 0.5.

**Head.** postpedicel yellowish.

**Thorax.** scutellum dorsally metallic green and ventrally yellow.

**Abdomen.** terga 1–2 metallic green with bronze reflections and some gray pruinosity; terga 3–5 brown with metallic green reflections; terga six and seven brownish or even yellowish; vestiture yellow; sternum eight brown with metallic green reflections; hypopygium dark brown with yellow cercus; epandrium (Fig. 4l) pyriform, narrowed distally; hypandrium (Fig. 4m)

subapically thickened with tapering apex; aedeagus (Fig. 4n) with distinctive open apex, encompassing 45 deg. angle; surstylus (Fig. 4o) with subapical bladelike seta, subtended basad by peg-like apically curved seta; cercus elongate and curved apically.

**Female.** not clearly associated.

**Remarks.** *Thrypticus chanophallus* is known from Amazonian Peru, and it was reared from the petioles of *Eichhornia crassipes*. The open 45 degree apical angle of the aedeagus is diagnostic, and is the source of the specific epithet (Greek, *chanos* = open mouth, and *phallus* = penis or aedeagus).

*Thrypticus chanophallus* is host sympatric with both *T. truncatus* and *T. circularis*, and has been reared with each species from *Eichhornia crassipes* at the same site.

### *Thrypticus romus* sp. n

**Type material.** Holotype, ♂, Paratypes 7 ♂, 8 ♀, BRAZIL: Mato Grosso do Sul: Corumbá, Bahía Tanagerina, 8.iii.1998, emerged from *Eichhornia azurea*, G. Vieira (USNM).

**Additional material.** ARGENTINA: 2 ♂, ♀, Formosa: Rd.11, 12km S Formosa City 24.ii.1998; 10 ♂, 23 ♀, Rd.11, 13km N Río Bermejo, 30.i.1998. Acc.2408; 12 ♂, 15 ♀, Rd. 81, 10 km W Formosa City, 11.iv.1998. Misiones: ♂, 3 ♀, Rd.12, Río Garupá, 23.iv.2000. BRAZIL: São Paulo: ♂, 4 ♀, Rd. BR116, 500m E road marker km 182 S, 20.iv.2000 (all emerged from *Eichhornia azurea*, H. Cordo, SABCL).

**Description.** Similar to *T. truncatus* except as noted: Male. Body length 1.4; wing 1.4 by 0.5.

**Head.** postpedicel mostly yellow, but brownish apically.

**Thorax.** scutellum without distinct yellow margin.

**Abdomen.** terga 1–4 metallic green with bronze reflections; tergum five becoming brownish distally; terga six and seven yellowish; hypopygium (Fig. 3a) brown with yellow cerci; epandrium pyriform, rather wide at base, but narrowed distally; hypandrium (Fig. 3b) apically blunt, rounded; aedeagus (Fig. 3c) apically cleft with two narrow parallel arms, lower arm longer; surstylus (Fig. 3d) with blade like seta with thickened setae basad and distad; cercus elongate, narrow and curved apically.

**Female.** oviscapt brownish, narrow; aculeus (Fig. 3e).

**Remarks.** *Thrypticus romus* is known from the Río Paraná drainage, the Brazilian Pantanal and São Paulo state, and the northernmost provinces of Argentina. All specimens were reared from the petioles of *Eichhornia azurea*. The specific epithet *romus* is from the Spanish, “romo,” meaning blunt, and refers to the blunt hypandrium.

### *Thrypticus azuricola* sp. n

**Type material.** Holotype, ♂, Paratypes 2 ♂, 2 ♀, BRAZIL: Río de Janeiro: Campos das Goitacazes, 17.iv.2000, emerged from *Eichhornia azurea*, H. Cordo. [holotype and ♂, ♀, paratypes (USNM); ♂, ♀, paratypes, (SABCL)]

**Description.** Similar to *T. truncatus* except as noted: Male. Body length 1.4; wing 1.3 by 0.5.

**Head.** postpedicel yellow and only brown apically.

**Abdomen.** terga 1–4 metallic green with bronze reflections; tergum five becoming brownish distally; terga six and seven yellowish; hypopygium (Fig. 3f) brown with yellow cerci; epandrium pyriform, rather wide at base, but narrowed distally; hypandrium (Fig. 3g) apically blunt, wide, rounded and somewhat thickened, club-shaped; aedeagus (Fig. 3h) broadened subapically, elongate, with distinct socketed hairs as shown, and apically cleft, with wide lower arm; surstylus (Fig. 3i) with wide blade like seta and with thickened setae basad and distad; cercus thickened and curved apically.

**Female.** oviscapt brownish, narrow; aculeus (Fig. 3j).

**Remarks.** *Thrypticus azuricola* is known only from type locality in Río de Janeiro state, Brazil, where it was reared from *Eichhornia azurea*, as the specific epithet implies. The elongate aedeagus (Fig. 3h) with its socketed hairs is diagnostic, and we know of no other case in the Dolichopodidae where setae are present on the aedeagus.

*Thrypticus azuricola* and *T. romus* appear to be closely related, as both have a blunt curved hypandrium, and are the only two member of the *truncatus* Group reared from *Eichhornia azurea*.

### *Thrypticus formosensis* sp. n

**Type material.** Holotype, ♂, Paratypes, 3 ♂, 5 ♀, ARGENTINA: Formosa: Rt 81, 20 km E Ibarreta, 14.iv.1996, emerged from petioles of *Pontederia*, Acc. 41222, H. Cordo (dry specimens on pins, USNM).

**Additional material.** ARGENTINA: Corrientes: 8 ♂, 7 ♀, Rd. 12, 5km E Ituzaingó acc. 27.vi.1998; 7 ♂, 4 ♀, Paso de la Patria, road to P. Gonzalez, 27.vi.1998. Formosa: 8 ♂, 5 ♀, Rd.81, 14km SE Ibarreta, 14.ii.1998; 6 ♂, 15 ♀, Rd.81, 2km W Cmte. Fontana, 23.iii.1998 (all emerged from *Pontederia cordata*, H. Cordo, SABCL).

**Description.** Similar to *T. truncatus* except as noted: Male. Body length 1.4–1.5; wing 1.5 by 0.6.

**Head.** major setae brownish; scape and external surface of pedicel yellow; median surface of pedicel and postpedicel brown.

**Thorax.** scutellum metallic green, with distinct dorsal yellow margin.

**Abdomen.** terga 1–4 metallic green with bronze reflections; tergum five becoming brownish distally; terga six and seven yellowish; hypopygium (Fig. 3k) brown with yellow cerci; epandrium pyriform, rather elongate and tapering distally; hypandrium (Fig. 3l) apically subovate, and tapering to sharp apex, and relatively short, not extending beyond epandrial lobes; aedeagus (Fig. 3m) apically cleft, with lower arm thickened and bent L-shaped across tip of upper arm; surstylus (Fig. 3n) rather wide in ventral view, with wide blade-like seta and with thickened setae basad; cercus elongate and curved apically.

**Female.** oviscapt brownish, narrow; aculeus (Fig. 3o).

Table 1. *Thrypticus* (Dolichopodidae) reared from Pontederiaceae host species

	<i>Eichhornia crassipes</i>	<i>Eichhornia azurea</i>	<i>Pontederia cordata</i>	<i>Pontederia subovata</i>	<i>Pontederia rotundifolia</i>
<i>Thrypticus truncatus</i>	Ar, Br, Pe				
<i>Thrypticus sagittatus</i>	Ar, Br, Tt				
<i>Thrypticus yanayacu</i>	Pe				
<i>Thrypticus circularis</i>	Ar, Pe				
<i>Thrypticus chanophallus</i>	Pe				
<i>Thrypticus romus</i>		Ar, Br			
<i>Thrypticus azuricola</i>		Br			
<i>Thrypticus formosensis</i>			Ar, Br		
<i>Thrypticus taragui</i>				Ar	(Pe?)

Ar, Argentina; Br, Brazil; Pe, Peru, Tt, Trinidad.

**Remarks.** *Thrypticus formosensis* is known from Formosa and Corrientes Provinces in subtropical northern Argentina. All known specimens emerged from petioles of *Pontederia cordata*. This species has darker coloration, especially on the abdomen, than the other members of the *truncatus* Group.

*Thrypticus taragui* sp. n

**Type material.** Holotype, ♂, Paratypes, ♂, 2 ♀ AR-GENTINA: Corrientes: Rd 12 Ituzaingó, 29.vi.1998, emerged from underwater stems of *Pontederia subovata*, H. Cordo. (USNM, dry pinned); 2 ♀, same but 27.vi.1998 (SABCL, in alcohol)

**Description.** Similar to *T. truncatus* except as noted: **Head.** major setae yellow; scape and pedicel yellow; postpedicel infuscated.

**Thorax.** scutellum metallic green, with distinct dorsal yellow margin.

**Abdomen.** terga 1–4 metallic green with bronze reflections; tergum five becoming brownish distally; terga six and seven yellowish; hypopygium (Fig. 4g) dark brown with yellow cerci; epandrium pyriform, narrowed distally; hypandrium (Fig. 4h) apically almost truncated; aedeagus (Fig. 4i) with thick lower apical arm which bends in L-shape in front of apex of narrower upper arm; surstylus (Fig. 4j) with blade like seta with thickened setae basad and distad; cercus elongate and curved apically.

**Female.** similar to male except face slightly wider; segment seven (forming oviscapt sheath) brown; oviscapt brownish, narrow; aculeus (Fig. 4k).

**Remarks.** *Thrypticus taragui* is known only from Corrientes Province, northern Argentina, and specimens were reared from the underwater stems (not petioles) of *Pontederia subovata*. The specific epithet is derived from “Taragui,” the indigenous Guaraní name for the Corrientes region. *Thrypticus taragui* is close to *T. formosensis* (reared from petioles of *Pontederia cordata*), and the two are possibly sister species, with species separation resulting from host switching on *Pontederia*.

A small series from Peru (4 ♂, 3 ♀, Peru: Río Kumasewa, 04°33'06" S 73°27'15" W 2.v.1999, emerged from petioles of *Pontederia rotundifolia*) is similar to *T. taragui* in hypopygial structure. However, the series has a slightly different aculeus, and was reared from the petioles of *Pontederia rotundifolia* (*T. taragui*

emerged from underwater stems of *P. subovata*). Possibly this series represents an additional species, but more specimens and information are required.

Bionomics

All material used in this study is the result of investigations into the biological control of water hyacinth, *Eichhornia crassipes*. Considerable effort and resources have been expended on this work, based at SABCL in Hurlingham, Buenos Aires. The nearby delta of the Río Paraná is the site for many observations, where the following species of Pontederiaceae are found growing together: *Eichhornia crassipes*, *E. azurea*, *Pontederia cordata*, and *P. rotundifolia*. In addition to field collecting, observations were made within walk-in rearing cages which measure (2 by 4 by 1.8 m) in the back yard of the SABC Laboratory. Inside these cages are pools with water hyacinth and smaller cages for detailed observations. In some cases the pupae are separated and incubated in complete or sectioned petioles, in separate rearing chambers. Cordo et al. (2000) and Hernández et al. (2004) provide a summary of previous investigations, with information on life histories, host damage, and potential for biological control. Further investigations are being conducted on *Thrypticus* larval biology by the second author.

**Host fidelity and sympatry.** Initially only one *Thrypticus* species was thought to be attacking plants of the family Pontederiaceae. However, careful investigations and rearing have revealed the nine species described here (Table 1), and five of them were reared from water hyacinth. Due to their abundance and geographic distribution, two of the species, *T. truncatus* and *T. sagittatus*, were chosen for further investigation. Both species have similar larval behavior and were reared only from *Eichhornia crassipes*. These species were tested for host range, both in the laboratory and in the field by interspersing test plants among infested water hyacinth plants. The two species, *Thrypticus truncatus* and *T. sagittatus* did not attack any of the following aquatic plants: *Eichhornia azurea*, *Pontederia cordata*, *P. rotundifolia*, *Echinodorus grandiflorus*, *Canna glauca*, and *Myriophyllum aquaticum*. This suggests that both species have potential as biological control agents, and warrant further investigation into their biology and specificity.



The extensive rearings, not only from *Eichhornia crassipes*, but also to a lesser degree from four other species of Pontederiaceae showed a high degree of host fidelity (Table 1) for all the *Thrypticus* species.

Since two or more *Thrypticus* species are often reared together, sympatry exists at both the site and host level. The following two sets of species occur sympatrically, and both have been reared from *Eichhornia crassipes* in the same collection event:

1. *Thrypticus sagittatus*, *T. truncatus*, and *T. circularis*: sites in northern Argentina and southeastern Brazil.
2. *Thrypticus truncatus*, *T. yanayacu*, *T. circularis*, and *T. chanophallus*: sites in the upper Amazon, Iquitos district of Peru.

It is not known if the two species occur together as larvae in a petiole of the same plant, and if so, if there is any distinct resource, behavioral or temporal niche differentiation. However, the larvae of some species are known to inhabit specific structures within their hosts. For example, *Thrypticus circularis* is found only in the globose inflated petioles of *Eichhornia crassipes*. These inflated petioles are distinct from normal petioles, and function as floats to facilitate vegetative dispersal. Further, *Thrypticus taragui* emerged from underwater stems (not petioles) of *Pontederia subvata*.

**Life history.** In both *Thrypticus truncatus* and *T. sagittatus*, the larvae bore a horizontal mine in the petiole, making a small incision in the vascular bundles and then feed on the exuded sap. Inside the mine, the larva moves back and forth, revisiting the damaged bundles and enlarging the larval cavity. The larva does not leave its mine, nor does it appear to have the ability to form another mine if transferred to a new petiole. The last instar digs a special pupation chamber sealed with an operculum of plant epidermis.

Adults are present from spring through to the end of summer. During autumn and winter no oviposition or new mines were recorded, and it is inferred both *Thrypticus* species spend the winter months as larvae in the petioles. In the summer, however, a generation of *T. truncatus* can be completed in  $\approx 7$  wk, with adults living for  $\approx 5$ –9 d. Adults usually rest on the basal part of the petioles under the water hyacinth canopy, making short flights up and down or between the petioles, but walking backwards to descend the petiole near the water.

**Mating behavior.** In laboratory conditions, female *T. truncatus* begin mating a few hours after emergence. After emerging, individuals usually remain on the petioles with their head up. Before mating, the male moves near the female and jumps repeatedly over her, up and down. In some of these jumps he rests for an instant on the female, and if she remains still, coupling takes place. The male introduces his hypandrium together with the aedeagus into the female genital atrium. The hypandrium acts as a guide for the aedeagus and may enter the female before the aedeagus. During coupling, with the hypandrium and aedeagus inside the female, the cerci and surstyli reach the third

abdominal sclerite, where they touch the abdomen rhythmically.

**Oviposition and eggs.** Females exhibit the following behavior which is probably oviposition, even though deposited eggs have not been found during careful microscopic searches: the female moves up the basal part of the petiole touching the surface with her oviscap, and then sometimes stops and bends the abdomen downwards. This is possibly the moment when an egg is inserted within the plant tissue. Eggs of *T. truncatus* were obtained by dissecting the female abdomen, and are 0.45 by 0.02 mm; whitish, cylindrical and slightly curved, with one end rounded and the other more pointed.

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